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Functional Response, Reproductive Function and Movement Rate of a Grazing Herbivore: The Citrus Rust Mite on the Orange

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Source: *The Florida Entomologist*, Vol. 75, No. 1 (Mar., 1992), pp. 72-83

Published by: [Florida Entomological Society](#)

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where  $f$  is the proportion of females in the population,  $L_{(a)}$  is the age-specific survivorship - or the probability that an individual is still alive at age  $a$ , and  $m(a)$  is the age-specific fertility - that is the rate of offspring production at age  $a$ . Apart from  $R_0$  we also need to know the mean age at child-bearing, from which  $\mu$  is defined as:

$$\mu = \frac{\alpha}{R_0} \int_0^{\infty} a L(a) m(a) da$$

Spatial spread is defined by the variance of the marginal density of the distances between a nesting bird and its parent's nest:

$$\sigma^2 = \int_0^{\infty} \int_0^{\infty} x^2 D(x,y) dx dy$$

where  $x$  and  $y$  are spatial coordinants and  $D$  the diffusion coefficient. Then, the expected velocity of population expansion becomes:

$$C_{exp} = \frac{\sigma}{\mu} \sqrt{2 \text{Log}_e(R_0)}$$

(van den Bosch et al. in press). Van den Bosch et al. (in press) applied this model to more extensive data; Hengeveld and van den Bosch (1991) show the actual calculations, and van den Bosch et al. (1990) give the mathematical derivations.



## FUNCTIONAL RESPONSE, REPRODUCTIVE FUNCTION AND MOVEMENT RATE OF A GRAZING HERBIVORE: THE CITRUS RUST MITE ON THE ORANGE

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### ABSTRACT

A model of the attack rate for a grazing herbivore, the citrus rust mite, is obtained as a Type 2 functional response analogous to Holling's disc equation. The attack rate is given by

$$A' = \frac{cx'}{1 + ct_h x'} \quad (\text{cells mite}^{-1} \text{d}^{-1})$$

where  $c$  is the maximum cell attack rate given by  $c = qv\sqrt{\delta}$ .  $t_h$ ,  $q$ ,  $v$  and  $\delta$  are the handling time  $\text{attack}^{-1}$ , probability of attack, the velocity while grazing, and the total cell density  $\text{cm}^{-2}$  respectively.  $x'$  is the proportion of the total cells which remain alive.  $A'$  needs to be multiplied by the proportion of time spent "grazing" if this is less than one. If  $y$  is the mite density in any area having perimeter/area ratio  $P/a$  then the emigration rate is given by

$$m' = \frac{P}{a} \frac{v}{1 + ct_h x'} y \quad (\text{mites cm}^{-2} \text{d}^{-1})$$

$m'$  also needs to be multiplied by the proportion of time spent grazing. Egg production rate,  $E$ , was assumed proportional to  $A'$  so that

$$E = E_{\max} \frac{A'}{A'_{\max}} = E_{\max} \frac{(1 + ct_h)x'}{1 + ct_h x'} \quad (\text{eggs d}^{-1})$$

where  $E_{\max}$  is the maximum egg production rate when food is maximum ( $x' = 1$ ).

#### RESUMEN

Se obtuvo un modelo de la rata de ataque de un herbívoro, el acaro tostador de los cítricos, como una respuesta funcional tipo 2 analoga a la ecuación de disco de Holling. La rata de ataque es especificada por:

$$A' = \frac{c x'}{1 + ct_h x'}$$

donde  $c$  es la rata de encuentro de la celula especificada como  $c = qv\sqrt{\delta}$ .  $t_h$ ,  $q$ ,  $v$  y  $\delta$  son el tiempo de ataque $^{-1}$ , la probabilidad del ataque, la velocidad de pastoreo, y la densidad total de la celula en  $\text{cm}^2$ , respectivamente.  $x'$  es la proporción de todas las celulas que permanencen vivas.  $A'$  necesita ser multiplicado por la proporción de tiempo dedicado a el pastoreo si es menos que uno. Si  $y$  es la densidad del acaro en cualquier area con un perimetro/proporcion area  $P/a$ , entonces la rata de emigración es especificada por

$$m' = \frac{P}{a} \frac{v}{1 + ct_h x'} y$$

$m'$  tambien necesita ser multiplicado por la proporción del tiempo dedicado a el pastoreo. La rata de producción de huevos,  $E$ , fué asumida como proporcional a  $A'$  de tal forma que

$$E = E_{\max} \frac{A'}{A'_{\max}} = E_{\max} \frac{(1 + ct_h)x'}{1 + ct_h x'} \quad (\text{eggs d}^{-1})$$

donde  $E_{\max}$  es la rata de producción máxima de huevos cuando el alimento esta al máximo ( $x' = 1$ ).

Whenever we attempt to model the attack of one species upon another, we are faced with the problem of how to construct a trophic transfer function describing the flow of material between the two species. These trophic coupling functions are commonly called the functional response of the "predator" species to the "prey" species density after the term used by Holling in his classical early work on the subject (Holling 1959a, 1959b, 1965). Many such functions have been suggested in the literature (May 1978, Table 5.1, gives a list of possibilities), but the major emphasis has been on true predator-prey rather than herbivore-plant interactions (Caughley & Lawton 1978, Noy-Meir 1975). The problem we discuss here is one of a herbivore, *Phyllocoptruta oleivora* (Ashm.) (the citrus rust mite), feeding on the surface of citrus fruit. Our objective is to derive expressions for the functional response in terms of fruit cells killed mite<sup>-1</sup> day<sup>-1</sup> as a function of the cells cm<sup>-2</sup> remaining alive, and to relate the functional response to the rates of movement and reproduction. While the rust mite is used as an example, the situation is rather general and could, with only slight modification, be applied to most grazing herbivores.

The citrus rust mite is a tiny eriophyid mite about 180 μm in length which feeds on individual epidermal cells on citrus fruit and leaves. For calculation purposes, we assume that the epidermal cells are about 10 μm in diameter, and the feeding punctures made by the mite are about 0.7-1.0 μm in diameter (McCoy & Albrigo 1975, Achor et al. 1991). Given the scale at which the attack occurs, one is tempted to take a "regression" approach as the senior author did in an earlier study (Allen 1976). It was found that visual estimates of the percent damage on the orange surface accumulated linearly with mite-days with the caveat that the slope increased with time in a roughly sigmoid fashion over the maturity cycle of the orange.

In the current paper, we adopt a more detailed **process**-oriented approach involving cells cm<sup>-2</sup> and mites cm<sup>-2</sup> as system variables whose interaction is to be modelled as part of a dynamic system which will ultimately include the mite fungal pathogen, *Hirsutella thompsonii* (Fisher) (Allen et al. in press). With the process-oriented approach, one can examine the possibility that the time-varying damage rate observed in the field was a result of cell expansion during fruit growth.

#### THE FUNCTIONAL RESPONSE OF A GRAZING HERBIVORE

Holling obtained his original "disc" equation by having a blindfolded subject search for sandpaper discs on a tabletop by tapping with one finger, and upon finding a disc, remove it and place it to one side (Holling 1959a). This process was used to model the attack rate (= functional response) of a predator, and the function exhibited a saturation effect (leveling-off) as the prey density became high. This was because the "predator" (subject) became saturated with "prey" and spent all the time just handling prey, i.e., time was assumed to be conserved and was divided by type of activity. Thus

$$T_s = T_t - At_h \quad (1)$$

where  $T_s$  is time spent searching for prey,  $T_t$  is total time and  $At_h$  is total time spent handling prey,  $A$  being the number of prey attacked and  $t_h$  being the handling time per attack. In addition it was assumed that

$$A = aT_sx \quad (2)$$

where  $a$  = proportion of available prey encountered (or area searched) per time unit, and  $x$  was the prey density. Upon substituting eq.(1) into eq.(2) and solving for  $A$  we obtain the now famous disc equation or Type 2 functional response

$$\frac{A}{T_t} = A' = \frac{ax}{1 + at_h x} \tag{3}$$

where we have written the equation with total time in the denominator on the left-hand-side so that we have the attack **rate** which we will call  $A'$ .

We now proceed to the case of a grazing herbivore moving with scalar velocity (unspecified direction)  $v$  over a food substrate which has density  $x$  per unit area. We will consider epidermal cells  $\text{cm}^{-2}$  in our study of the rust mite, but one could talk about plants or mass per unit area just as well. As our herbivore moves over the substrate, the number of "prey" encountered is equal to the distance covered ( $vT_s$ ) divided by the average distance between prey ( $d$ ). In the rust mite situation the cells are relatively uniform in their spatial distribution and we assume a mean cell diameter of about 10  $\mu\text{m}$  and consequently a cell density of about  $10^8 \text{ cm}^{-2}$ . Contagious (i.e., clumped) distributions of plants or other resource objects might be handled by combining the approach used here with the negative binomial probability of being found (1 - zero class) as per Holling (1988). In our case

$$\text{Number of Cells Encountered} = \frac{\text{Distance Covered}}{\text{Mean Cell Diameter}} = \frac{vT_s}{d},$$

but at least approximately

$$\text{cell density} = \delta = \frac{1}{d^2}$$

so  $d = \frac{1}{\sqrt{\delta}}$ , and therefore the Number of Cells Encountered =  $vT_s \sqrt{\delta}$ . We now assume

Cells Attacked = (Probability of Attack) (Cells Encountered) (Proportion Alive)

or in symbolic form

$$A = qvT_s \sqrt{\delta} \frac{x}{\delta} = qvT_s \sqrt{\delta} x' \tag{4}$$

where  $q$  is the probability of attack and  $x'$  is the proportion alive. Since time is conserved

$$T_s = T_t - At_h - T_o \tag{5}$$

where  $T_o$  is time spent on activities other than searching and feeding. By substituting eq.(5) into eq.(4) we obtain

$$\frac{A}{T_t} = A' = \frac{qv \sqrt{\delta} (1 - \frac{T_o}{T_t})x'}{1 + qv \sqrt{\delta} t_h x'} \tag{6}$$

where  $(1 - \frac{T_o}{T_t})$  is the proportion of time spent on "grazing", i.e., the feeding-moving cycle, and the extension of the disc equation, eq.(3), is obvious. Much of the attraction

of eq.(6) is that for many herbivores the parameters can be obtained by independent observation. For example, McCoy & Albrigo (1975) observed that rust mite "searching" time averaged  $11.3 \pm 7.3$  s and mouthpart insertion time averaged  $26.0 \pm 20.0$  s. Although these measurements are just a crude beginning, they serve as an example that the parameters of eq.(6) can be obtained by direct observation even for an animal as small as the rust mite.

We assume that eq.(6) represents the attack rate  $\text{mite}^{-1}$ , and therefore the total mortality rate for cells under attack by  $y'$  mites  $\text{cm}^{-2}$  is eq.(6) multiplied by  $y'$ . If we now plot eq.(6) for different mite and cell densities, the form of the classical Type II functional response emerges (Fig. 1). The  $\frac{T_o}{T_o}$  ratio is held constant at 0.5 (this is simply a

guess), and cell encounter rate and handling time are varied to illustrate the effect of these parameters on the placement and shape of the curve. We hasten to emphasize that the exact placement of the curve is not known to any great degree of certainty, and the values shown are simply order-of-magnitude estimates from what little is known.

Field estimates of damage rates ( $\% \text{ mite}^{-1} \text{ d}^{-1}$ ) by visual inspection of fruit surfaces indicate that the damage rate increases with fruit maturity from about 0.001% to 0.01%  $\text{mite}^{-1} \text{ d}^{-1}$  (Fig. 5) and (Allen 1976). The curves of Fig. 1 assume a cell density of  $10^6 \text{ cm}^{-2}$  and their maxima (when  $x' = 1$ ) vary from about 100,000 to 30,000 cells  $(100 \text{ mites})^{-1} \text{ d}^{-1}$  which corresponds to 0.1% to 0.03%  $\text{mite}^{-1} \text{ d}^{-1}$ . Thus, the parameters used in Fig. 1 give cell mortalities which, on a percentage basis, are at least 3-fold larger than observed visual estimates of % damage from the field. This apparent disagreement may simply mean that *visual* % damage is not equal to % cell mortality, i.e., the model may be "right" and the visual data may be "wrong"! Alternatively,  $q$  or  $v$  may be too large or the proportion of time spent feeding  $(1 - \frac{T_o}{T_t})$  may be too large. Regardless of parameter uncertainty, eq.(6) finally gives us a mechanistic model of the interaction between the mite and the fruit for which data can be obtained by direct observation of the feeding process.

#### A MOVEMENT RATE FUNCTION FROM THE FUNCTIONAL RESPONSE

When modelling populations, it is often of interest to have a submodel of movement into and out of some spatial region of interest, a field, a leaf, or a unit of area. We will consider the rust mites emigrating from a  $\text{cm}^2$  of fruit surface. We assume that the number of mites moving across one side of the  $\text{cm}^2$  is proportional to their velocity,  $v$ , the time spent searching,  $T_s$ , and their density,  $y$ . The effect of this movement on the **density** in the  $\text{cm}^2$  is 4 times this amount however, since there are 4 sides, and in general, one needs to multiply the movement across a unit of boundary by the perimeter/area ( $P/a$ ) ratio (= 4 in a square unit of area) (Brewster & Allen 1991). Thus, the total emigration effect on density in our case is

$$m = \frac{P}{a} v T_s y \quad (\text{mites cm}^{-2})$$

But, since  $T_s = T_t - A t_h - T_o$ , and  $A = c T_s x'$  where  $c = qv \sqrt{\delta}$ , then

$$T_s = \frac{T_t - T_o}{1 + c t_h x'}$$

and our density change due to emigration from the  $\text{cm}^2$  becomes

Cell Mortality From Citrus Rust Mite Feeding

cell density =  $10^6 \text{ cm}^{-2}$

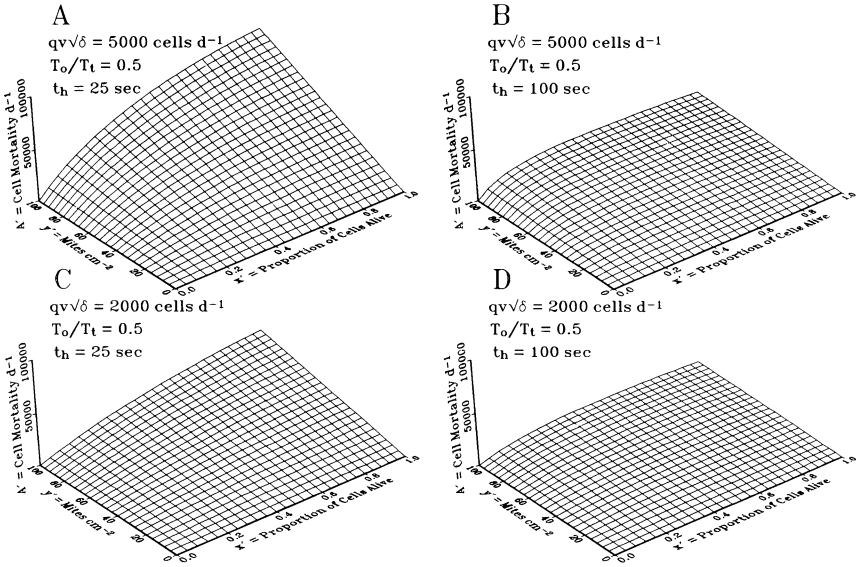


Fig. 1. The attack rate (functional response) of the citrus rust mite on citrus epidermal cells. Cell density is expressed as proportion of  $10^6$  cells  $\text{cm}^{-2}$ .  $y'$  is the density of all feeding stages of the mite  $\text{cm}^{-2}$ . From eq.(6) in the text.

$$\frac{m}{T_t} = m' = \frac{P}{a} \frac{v(1 - \frac{T_o}{T_t})}{1 + qv\sqrt{\delta} t_h x'} y \quad (\text{mites cm}^{-2} \text{d}^{-1}) \quad (7)$$

We look at this graphically as a function of rust mite and cell densities in Fig. 2, where the parameter values are identical to those of Fig. 1, and we note that the more saturated (leveled-off) is the functional response of Fig. 1, the more nonlinear is the emigration rate (eq.(7)) as food diminishes (Figs. 1B and 2B). Of course, what we would really like is the net change in density in our  $\text{cm}^2$ , and so we must calculate the difference between input and output using eq.(7) and take the difference. The price one pays for this is that the densities outside the  $\text{cm}^2$  must be known or modelled.

A REPRODUCTIVE RATE FUNCTION FROM THE FUNCTIONAL RESPONSE

We assume that egg production by our herbivore (the rust mite) is proportional to food intake up to some maximum egg production rate ( $E_{\max}$  when  $x' = 1$  in eq.(6)). In general

$$\text{eggs d}^{-1} = (\text{eggs attack}^{-1}) (\text{attacks d}^{-1})$$

or symbolically

Movement Rate Function for Citrus Rust Mite

cell density =  $10^6 \text{ cm}^{-2}$

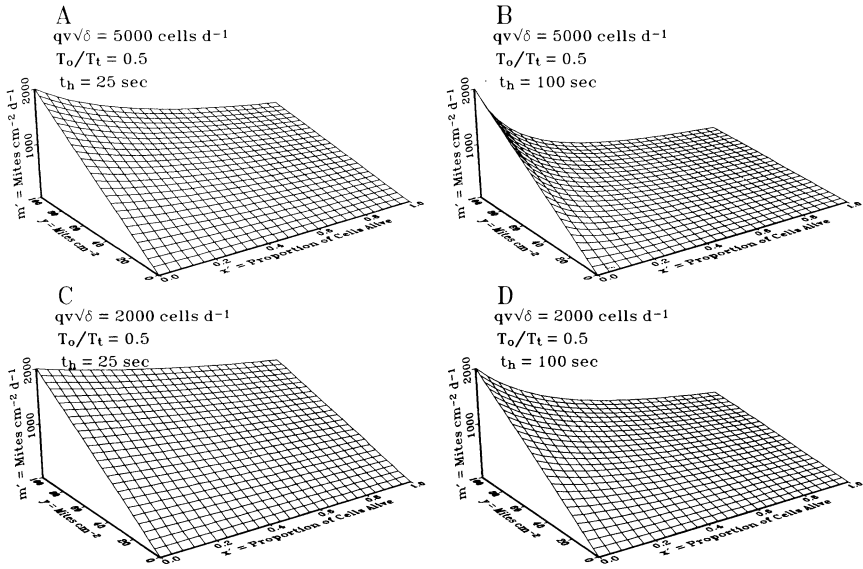


Fig. 2. The movement rate out of a  $\text{cm}^2$  containing living cell proportion  $x'$  by mites at density  $y \text{ cm}^{-2}$ . Parameters are identical to Fig. 1. From eq.(7) in the text.

$$E = \epsilon A' = \epsilon \frac{cx'}{1 + ct_h x'}$$

where  $c = qv \sqrt{\delta}$ .  $\epsilon$  can be obtained from observed maximum egg production rates when  $x' = 1$ , i.e.,  $\epsilon = \frac{E_{\max}}{A'_{\max}}$  where  $A'_{\max}$  is eq.(6) with  $x' = 1$ . By substituting for  $\epsilon$  in the above equation the reproductive rate becomes

$$E = E_{\max} \frac{A'}{A'_{\max}} = E_{\max} \frac{(1 + ct_h)x'}{1 + ct_h x'} \tag{8}$$

Note that we have tacitly assumed for simplicity that  $(1 - \frac{T_o}{T_t})$  cancels in the ratio of attack rates in eq.(8), i.e., that proportion of “other” time is the same regardless of the food supply (an assumption which needs to be checked). We currently have the total egg output over the life of a female rust mite as a function of temperature ( $T$ ) ( $^{\circ}\text{C}$ ) given by

$$\text{total eggs} = 66.811 - 11.979T + 0.69897T^2 - 0.011925T^3$$

and the length of the reproductive period is given by

$$\text{adult time} = 29.74e^{-0.0743T}$$



Reproductive Function for the Citrus Rust Mite

cell density =  $10^6 \text{ cm}^{-2}$

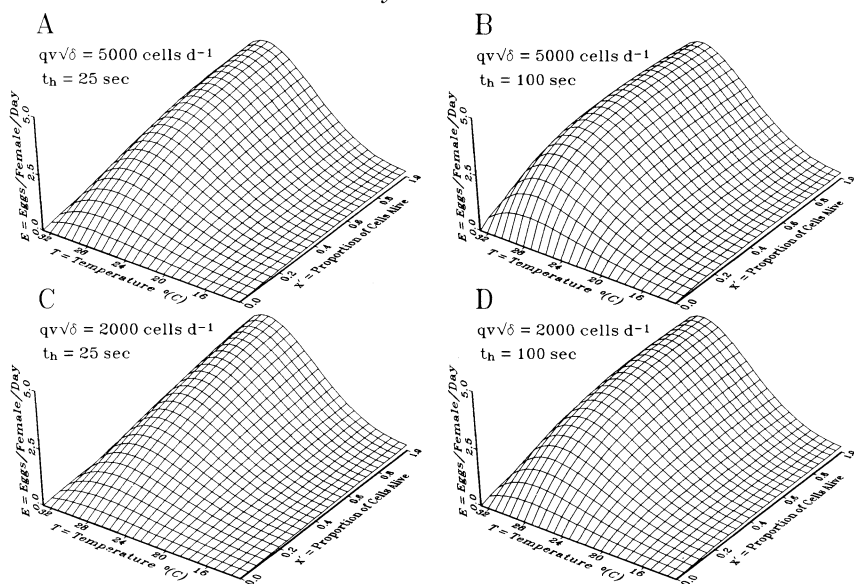


Fig. 3. The reproductive rate of the citrus rust mite (eggs female<sup>-1</sup> d<sup>-1</sup>) as a function of temperature and proportion of epidermal cells alive. Parameters are identical to Fig. 1. From eq.(8) in the text.

so the average adult egg production rate is given by  $E_{\max} = \frac{\text{total eggs}}{\text{adult time}}$  from laboratory

data where we assume  $x' = 1$ . Using this as our  $E_{\max}$ , we plot the reproductive rate from eq.(8) in Fig. 3 over the temperature range of 13 to 33°C. These curves have a maximum at about 28°C of 4.8 eggs female<sup>-1</sup> d<sup>-1</sup> when living cell density is maximum ( $x' = 1$ ) and drop off in somewhat different ways with declining food supply depending on the details of the functional response parameters. Again we hasten to emphasize the approximate and preliminary nature of these curves due to omission of some factors (e.g., differences in  $T_o$  with food supply and sex ratio effects) and outright guesses at others (e.g.,  $q = 0.5$  and  $v = 10 \text{ cm d}^{-1}$ ), nevertheless they serve as a starting point for a model of this system and indicate where data are needed.

WHAT DATA ARE NEEDED TO IMPROVE THE ACCURACY OF THESE FUNCTIONS?

Throughout the development of eqs.(6), (7) and (8) it was assumed that epidermal cell density,  $\delta$ , was known, e.g., in Figs. 1, 2 and 3 it was assumed that cell diameter was about 10  $\mu\text{m}$  and therefore that  $\delta$  was about  $10^6 \text{ cells cm}^{-2}$ . This was based on estimates by McCoy & Albrigo (1975) that “epidermal cell thickness ranged from 6-12  $\mu\text{m}$ ” and by micrographs in their paper suggesting cell diameters of about 10  $\mu\text{m}$ . In addition, leaf epidermal cell sizes appear to be on the order of 10  $\mu\text{m}$  (Achor et al. 1991). However, it is known that fruit epidermal cells stop dividing and undergo an expansion phase in the later stages of fruit growth (Bain 1958). In addition, recent preliminary

measurements indicate that **mature** grapefruit and navel oranges have epidermal cell diameters of 40-80  $\mu\text{m}$  (D. Achor, pers. communication). Good measurements of fruit surface area ( $S$ ) are available for Valencia orange (Allen 1976) where it was found that

$$S(t) = \frac{k}{1 + e^{\alpha - \beta t}} \quad (9)$$

in  $\text{cm}^2$  where  $t$  is days since 1 Jan. of the starting year,  $k = 153 \text{ cm}^2$ ,  $\alpha = 4.8$ , and  $\beta = 0.03592 \text{ d}^{-1}$ . Could cell expansion be proportional to surface expansion and therefore cell density be some inverse form of this sigmoid growth function? If we assume that cell density starts at  $\delta_{\text{max}}$  and ends at  $\delta_{\text{min}}$ , and decreases as the inverse of surface expansion, then we can write an equation for cell density with time as

$$\delta(t) = (\delta_{\text{max}} - \delta_{\text{min}}) \frac{e^{\alpha - \beta t}}{1 + e^{\alpha - \beta t}} + \delta_{\text{min}} \quad (10)$$

where the exponential fraction part is the inverse of eq.(9), i.e.,  $\delta(t)$  declines in sigmoid fashion from  $\delta_{\text{max}}$  to  $\delta_{\text{min}}$  in phase with fruit surface expansion from eq.(9). The % damage  $\text{mite}^{-1} \text{ d}^{-1}$  should now be given by  $\frac{A'}{\delta(t)}$  (100), and using eqs.(6) and (10) to calculate this ratio, the result is plotted in Fig. 4 against time of year for comparison with **visual** %

### Effect of Cell Expansion on % Damage $\text{Mite}^{-1} \text{ Day}^{-1}$

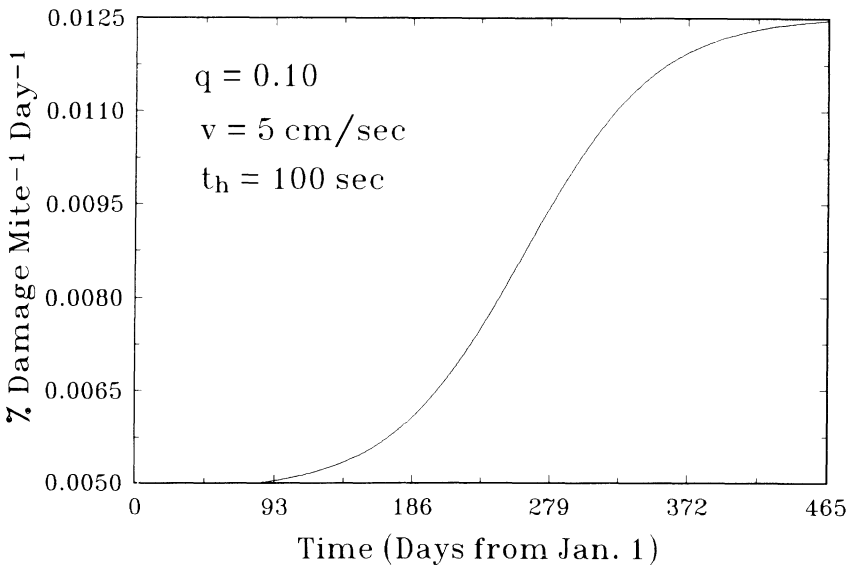


Fig. 4. The attack rate of the mite expressed as % damage  $\text{mite}^{-1} \text{ d}^{-1}$  varying through time due to epidermal cell expansion during fruit growth. Obtained by dividing eq.(6) by eq.(10) and multiplying by 100. (Compare with Fig. 5).

damage estimates from the field in Fig. 5 (reprinted from Allen 1976). We assumed that  $\delta_{\max} = 2 \times 10^6$  and  $\delta_{\min} = 5 \times 10^5$  cells  $\text{cm}^{-2}$  respectively, and parameters as shown in Fig. 4 were chosen to give a fairly low attack rate. Thus one can, by appropriate choice of parameters, generate the time-varying damage rate effect much like that observed in the field from cell expansion alone.

This exercise does not prove that the time-varying damage rate observed visually in the field is strictly due to cell expansion, but it does illustrate what we can do once more accurate information is available on cell density with time,  $\delta(t)$ . Thus, the models developed here indicate what data are needed in the rust mite system before models of the system can be reliable tools for population dynamics studies and economic predictions.

Finally, in the more general case of a grazing herbivore, we have developed a functional response equation (eq.(6)) which is analogous to Holling's disc equation (eq.(3)). The constant  $a$  in the disc equation is equal to  $qv\sqrt{\delta}$  in our case of uniformly distributed cells.

In the case of **randomly** distributed plants at density  $x$ , the mean distance between them is  $\frac{1}{2\sqrt{x}}$  (Clark & Evans 1954), and the functional response of a grazing herbivore becomes

$$\frac{A}{T_t} = A' = \frac{2qv\sqrt{x}}{1 + 2qvt_h\sqrt{x}}$$

Except for the factor 2, this is our eq.(6) without considering "other" time ( $T_o$ ) or proportion of plants alive ( $x'$ ). Thus one obtains basically the same functional response

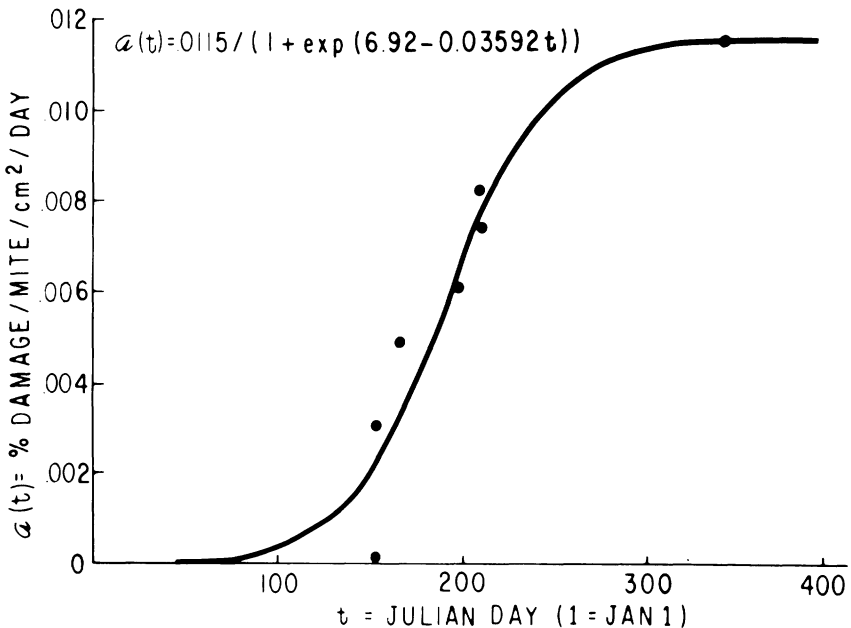


Fig. 5. % damage  $\text{mite}^{-1} \text{d}^{-1}$  by visual observations in the field. From Allen (1976). Reprinted with permission from the ESA.

TABLE 1. LIST OF VARIABLES AND PARAMETERS USED IN THE MODELS.

Variable/Parameter	Description	Units
$a$	proportion of area searched	$d^{-1}$
$A$	number of attacks during $T_t$	attacks
$A'$	attack rate ( $A/T_t$ )	attacks $d^{-1}$
$A'_{\max}$	maximum attack rate	attacks $d^{-1}$
$\alpha$	fruit growth constant	none
$\beta$	fruit growth rate constant	$d^{-1}$
$d$	mean cell diameter	cm
$\delta$	cell density	cells $cm^{-2}$
$\delta_{\max}$	maximum cell density	cells $cm^{-2}$
$\delta_{\min}$	minimum cell density	cells $cm^{-2}$
$E$	egg production rate	eggs female $^{-1} d^{-1}$
$E_{\max}$	maximum egg production rate	eggs female $^{-1} d^{-1}$
$\epsilon$	eggs produced attack $^{-1}$	eggs attack $^{-1}$
$k$	final fruit surface area	$cm^2$
$m$	density change due to movement	mites $cm^{-2}$
$m'$	movement rate	mites $cm^{-2} d^{-1}$
$P/a$	perimeter/area ratio	$cm^{-1}$
$q$	probability of attack	none
$S(t)$	fruit surface area	$cm^2$
$t$	days since 1 Jan.	d
$t_h$	handling time attack $^{-1}$	d
$T_t$	total time	d
$T_s$	searching time	d
$T_o$	"other" time	d
$T$	temperature	$^{\circ}C$
$v$	"grazing" velocity of rust mite	$cm d^{-1}$
$x$	living epidermal cell density	cells $cm^{-2}$
$x'$	proportion cells alive ( $x/\delta$ )	none
$y$	density of mite moving stages	mites $cm^{-2}$
$y'$	density of mite feeding stages	mites $cm^{-2}$

for either uniform or random resource units (plants, cells, etc.). We will leave for future research the question of a **clumped** distribution of resource units. . . .

#### ACKNOWLEDGMENTS

We would like to thank C. S. Holling, J. W. Jones, and H. L. Cromroy for their comments on the manuscript. D. S. Achor did some last-minute measurements on citrus fruit epidermal cell density from her lunchbox which indicate the need for more information on cell density. The patience of J. Howard Frank was much appreciated. We are also grateful to Julio Arias for translating the abstract into Spanish. This is Florida Agricultural Experiment Station Journal Series No. R-02104.

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